Roles of Microflora And Fauna in Soil Systems

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Introduction

From an ecosystem viewpoint, the primary role of soil microflora and fauna lies in their functions as decomposers and reducers. Autotrophic producers and heterotrophic consumers return their products and their bodies to the soil in the form of dead organic matter. Soil organisms reduce or decompose this organic litter; this action releases nutrients for reutilization by producers, yields organic byproducts such as humus and supports an array of saprovorous and carnivorous species. In this overview other important processes must be included – mineralization, nitrogen fixation, nitrification, symbiotic activities of the microflora and the mechanical fragmentation, mixing, and channeling and aggregate-forming actions of the soil animals. All of these processes combine to maintain the fertility of the soil system.

Faunal and microfloral communities in soils are structurally and functionally complex. Indirect methods are needed for estimating population turnover by soil microbes (Brock, 1966). Despite advances in methods of sampling (Edwards et al., 1970a; Aucamp, 1967) and community description (Wiegert et al., 1969), arthropod communities in soils remain poorly understood. Taxonomies, especially for the soil fauna of North America, are inadequate. Feeding habits of many soil arthropods are little known. Food chains in soil consist of loosely coupled trophic levels, which are complicated by influxes of consumer animals from above ground and the heterogeneous food bases of saprovores. It is now widely held that functional processes within the soil result from interactions between microflora and fauna (e.g. Doeksen et al., 1963). However, current concepts of the extent of these interactions and the magnitude of the interdependencies remain vague.

Measurements of dynamic processes in soils, which reflect or are governed by the combined action of soil fauna and microflora, are especially pertinent ~~to attempts~~ to evaluate influences of stresses such as pesticides. Respiration and energy flow in soils are examples of such inclusive processes, although microflora alone are responsible for some 90 percent of soil respiration (Phillipson, 1966). Losses of weight or minerals from decomposing litter are key processes resulting from the interactions of microflora and fauna. These losses are measurable experimentally and are influenced by pesticide contamination. Changes in rates of these processes indicate important changes in the soil system. Exchanges of minerals and energy along food chains in the soil are being measured by radioactive tracer techniques, and rates of these trophic exchanges are also indices of system functions. Experimental studies using techniques of systems analysis applied to microcosms (Patten et al., 1967) are especially promising since they allow for an evaluation of intact systems subject to manipulation and perturbations.

Litter Breakdown and Decomposition

Rates of litter breakdown

Organic materials reaching the soil surface lose weight, energy and minerals due primarily to attacks by microflora and fauna. The term "breakdown" is used here to denote the general process of disappearance of litter. "Decomposition" is reserved for the special action of microflora which are responsible for nearly all of the degradation of more complex organic molecules.

Several recent studies have used leaf litter confined in mesh bags to measure rates of weight loss under normal and experimental conditions (Edwards et al., 1963; Olson et al., 1963). In such studies, disappearance measured during the first year ranges from about 40 percent to 90 percent of initial weight, depending upon species and locality (Edwards et al., 1970a). Experiments with bagged litter and unconfined litter (Witkamp et al., 1963) often demonstrate a nonlinear rate of weight loss during the first year. Typically, loss rates are rapid initially, perhaps due to leaching of soluble materials. An intermediate slower phase of weight loss during winter months is followed by an accelerated loss rate during spring and summer. However, some reports (Edwards et al., 1963; Madge, 1969) document a more rapid rate of disappearance in winter than in spring and summer. Edwards et al. (1963) and Satchell et al. (1969) suggest that fresh leaf litter remains unpalatable to soil fauna until poly-

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phenols become leached out. Olson (1963) assumed that the fraction of litter remaining undecomposed was a negative exponential function, so that weight losses from litter would be a constant fraction (k) of the weight of litter remaining.

Interactions of biota in litter breakdown

Contributions of animals to the breakdown process (Edwards et al., 1970a) are several. Extensive incorporation of litter into the mineral soil may result from the feeding activities of earthworms (Satchell, 1967). Other soil animals such as millipedes and even microarthropods (Crossley et al., 1962) facilitate incorporation of litter fragments into the mineral soil. Recent reviews (Edwards et al., 1970a; Raw, 1967; Ghilarov, 1963; Kevan, 1962) emphasize that the most important contribution of the fauna appears to be the fragmentation of litter, both through mechanical breakage and by passage through the gut and conversion to feces. Most soil fauna lack the digestive enzymes which attack cellulose or lignin, but many evidently support symbiotic microbes which can degrade these materials (Hartenstein, 1962; Kevan, 1962). However, leaf litter appears to be little changed chemically during conversion to feces (Dunger, 1963; Bocock, 1963). Conversion to feces serves to fragment the litter, inoculate it with a microflora and often to incorporate mineral soil into contact with the litter. Fecal pellets may support a higher density of microbes than does the parent litter or the surrounding mineral soil (Ghilarov, 1963), and show high respiratory activity during the initial 14 days (Nicholson et al., 1966; Van der Drift et al., 1959).

Microflora and fauna in soil and litter habitats may have a closer symbiotic relationship than has been generally supposed. Evidence is increasing to support the view that essential, symbiotic intestinal microfloras are prevalent in the Arthropoda (Gordon, 1968). Soil fauna may play an active role in dissemination of propagules and in preparation of substrates (Macfadyen, 1963). Recently Mason et al. (1969) showed that passalid beetles (*Popilius disjunctus*), which tunnel in decaying wood, regularly ingest fecal materials; if deprived of feces, they lose weight and die. These authors suggest that the tunnel of the passalid beetle serves as an "external rumen"; wood ingested by beetles is fragmented and inoculated with microflora during passage through the gut. Microflora convert fecal materials to useable forms which the beetles assimilate when feces are ingested. The external rumen analogy may be applicable to the entire forest floor. Successive ingestion and re-ingestion of organic litter may be the mechanism whereby saprovores derive an energy and nutrient supply from a substrate which they cannot themselves digest.

Litter breakdown as a measure of system function

Litter breakdown results from the sum of the activities and interactions of soil biota, and thus litter breakdown rate constitutes a useful measure of system function. Crossley et al. (1962) and Olson et al. (1963) compared breakdown rates and populations of soil fauna in bagged leaf litter interchanged between a pine and an oak woods. Oak (*Quercus falcata* Michx.) and dogwood (*Cornus florida* L.) leaf litter lost weight more rapidly in the oak woods than in the pine woods. Dogwood litter decomposed more rapidly than oak litter. Weight loss by pine (*Pinus virginiana* Mill.) needles was slower than that of deciduous leaves. Needles lost weight at approximately the same rate in the two stands of trees. Microfauna (Acarina and Collembola) were more abundant in bagged litter in oak woods than in pine woods. Populations were higher in the more rapidly decomposing litter species. A succession of soil mite species appeared in the litter bags, and developed more rapidly in the litter with most rapid breakdown (dogwood).

Such essentially descriptive studies have been augmented by utilization of treatments to manipulate soil fauna populations. In experimental studies on litter decomposition, massive applications of an insecticide (naphthalene) were used by Kurcheva (1960) to reduce the numbers of soil fauna. In naphthalene-treated plots, oak (*Quercus rober* L.) leaf litter lost only 9 percent of its weight during a six-month period, compared with 55 percent weight loss in untreated control plots. Kurcheva attributed this large difference to the absence of invertebrate soil fauna in the treated areas. Crossley et al. (1964) and Witkamp et al. (1966) obtained less dramatic but similar results with naphthalene. Influences of naphthalene on populations of microflora were not measured in these experiments. Recently, Edwards et al. (1969) proposed a combination of insecticide (aldrin), fumigant (dichloropropene) and extractant (formalin) for reducing various segments of the soil fauna with minimal effects on the soil microflora. That system provides a method whereby several segments of the soil fauna can be reduced simultaneously or independently, and the subsequent effects on rate of litter breakdown can be used to assess the relative importance of different elements of the soil fauna. Gamma irradiation of experimental areas may be used to reduce both the soil fauna and soil microflora, and this technique has been proposed (Coleman et al., 1966) as an experimental tool for the study of processes in the litter-soil system.

Mineral Cycling

Loss of nutrient minerals from decomposing litter, like loss of weight, is strongly influenced by activities of microflora and fauna in soils. In those ecosystems in which litter constitutes an important storage reservoir for minerals, the activities of the litter-soil biota may control the rate of mineral cycling by controlling rates of mineral release from the litter. Rates of such releases, therefore, may be used as variables in experiments to assess the influences of fauna and microflora in soils.

Witkamp et al. (1966) measured the loss of radioactive ^{134}Cs from litter bags containing oak (*Quercus alba* L.) leaves, in areas treated with naphthalene and control areas, as a part of the litter breakdown experimentation mentioned above. Cesium, an analog of potassium, was found to be rapidly lost from leaf litter, presumably by leaching. In control plots, litter bags retained about 6 percent of the initial content of ^{134}Cs after 10 months. In plots from which arthropods had been excluded with naphthalene, litter bags retained about 15 percent, roughly twice as much of the initial ^{134}Cs content. Fractional loss rates k, (Olson, 1963) were 4.93 percent per week for control plots, and 2.95 percent per week for plots heavily treated with naphthalene. Berlese extractions of litter bags demonstrated that arthropod populations in treated areas were reduced to about 20 percent compared to those in control areas. Weight loss rates averaged 1.1 percent per week in control areas, and about 0.7 percent per week in naphthalene treated areas. The authors suggest that losses of ^{134}Cs in excess of weight losses were due to increased leaching. Activities of the arthropods by fragmenting leaf litter increase the surface area, thus enhancing the leaching action of moisture. Fragmentation, apart from actual ingestion, thus may exert a considerable influence on mineral releases from decomposing litter.

Little is known of the actual elemental contents of the soil fauna or their rates of mineral turnover. This information will be needed for further interpretation of the effects of fauna on mineral cycling. Edwards et al. (1970a) summarize available information on mineral content in some soil arthropods. Nutrient cycling is the topic of another paper (Goring) in this Symposium.

Food Web Dynamics

The soil biota is a complex assemblage of animal and plant groups whose feeding interrelationships remain poorly understood. Above-ground communities are rather easily separated into producers, herbivores and carnivores. Some groups occupy more than one trophic level, but generally, a linear food chain model adequately describes the trophic structure. In contrast, soil communities appear to resemble those of near-shore aquatic environments (Darnell, 1968) which are also detritus-based. Trophic levels appear to be less distinct than in grazing food chains, due in part to our inadequate knowledge of feeding habits and nutritional requirements of many species. Evidently some species may shift to different food bases as these become available, or at least can utilize a variety of materials as food. Predators have an alternate food source in herbivores from the above-ground parts of the ecosystem as these enter the soil to overwinter, pupate or oviposit. Root feeding herbivores are a small but possibly important part of the soil biota. For most detritus-feeding animals, a major question remains the extent to which the detritus alone or its microbial flora furnish the major part of nutritional requirements. Interpretations of the functioning of the soil biota and its reactions to stresses ultimately will require an understanding of the dynamics of such complex food webs. Current research on food webs is following three general approaches: energy flow, radioactive tracer analyses and systems analysis of microcosm experiments.

Energy flow and producticity

Energy flow has become the major unifying theme of modern ecosystem ecology. Odum (1968) has recently reviewed the historical development of the concepts of energy flow in ecology. For the food web of soil biota, Engelmann (1966, 1968) has provided conceptual models based upon the pioneering study of Lindeman (1942). A major part of energetics studies has been the measurement of respiration rates and biomasses. From these, energy expenditures by populations of soil biota may be calculated. Other aspects of flow, production and ingestion-assimilation by populations, are more difficult to measure.

Production in populations of consumers (heterotrophic productivity) is generally regarded as the storage of energy by those organisms. As Macfadyen (1967) emphasizes, usages and definitions differ, however. The measurements required include a knowledge of both weight gains by growing individuals, new births, and losses to mortality.

For communities in soil, such detailed information is available for few species, and broad assumptions are included in studies of energy flow.

Rates of ingestion and assimilation of energy often are the least known quantitites in an energy budget. Assimilation is usually calculated as the difference between energy ingested and energy lost in defecation. It requires careful budgets of food ingested and feces produced, and hence is almost always a laboratory study. Rates of ingestion may be measured in the laboratory, but often are poorly known for field populations.

Despite these limitations estimates of energy flow are exceedingly valuable for interpreting the food web. Energy flow is a valid basis for comparison and evaluation of diverse communities. Laws of thermodynamics assert that energy is an ultimate limiting factor in food webs. Further advances in understanding the energetics of the food web in soil will probably require the use of additional techniques, such as radioactive tracer methods, as well as improvements in conceptual models (Engelmann, 1968).

Radioactive tracer techniques

Radioactive tracers are a comparatively new ecological tool which nevertheless is finding increasing applications in trophic analysis under field conditions. Radioisotopes have been used in food web studies to identify feeding exchanges (Wiegert et al., 1969) and to measure rates of feeding (Crossley, 1966; Reichle et al., 1965). For rate measurements, an input-loss model is utilized, in which the accumulation of radioactive tracer is described as the difference between ingestion (input) and losses due to excretion.

Biological turnover (excretion) is usually measured by administering a single or short term feeding of radioactive tag, and then following the decrease in radioactivity in the animal. After corrections for radioactive (physical) decay, the decrease in radioactivity may be described by the equation:

$$A_t = A_o e^{-kt} \qquad (1)$$

where, A_t is the radioactivity of the animal at time t, A_o is the initial radioactivity of the animal following feeding on the radioactive tag, e is the base of the natural logarithms, and k is the loss rate coefficient. The loss rate is sometimes expressed as a biological half-life (T_b), the time required to lose 50 percent of the whole body radioactivity by biological means, and is given by:

$$T_b = \frac{\log_e 2}{k} \qquad (2)$$

Turnover rates are usually measured in the laboratory, but since they are functions of temperature, the results can be applied to field measurements (Reichle, 1967).

With continual feeding upon radioactive foods, animals accumulate radioactivity as described by the equation:

$$A_t = \frac{I}{k} \left(1 - e^{-kt} \right) \qquad (3)$$

where I is the rate of ingestion of radioactive tag. An equilibrium (Q_e) is reached when ingestion is balanced by loss, and A_t then fluctuates around a mean. At that time $Q_e = I/k$.

Reichle et al. (1965) analyzed soil and litter arthropods in a forest stand tagged with ^{137}Cs. Equilibria (Q_e) were estimated from samples for a variety of species. Turnover rates (k) were measured in laboratory conditions and corrected to field temperatures. From these, intakes (I) of ^{137}Cs were estimated and expressed as litter equivalents. Similar radioisotope estimates of feeding rates have been reported for forest canopy (Reichle et al., 1967) and herbaceous ecosystems (Crossley et al., 1961; Crossley, 1966).

Recently Kowal (1969) used radioisotopes ingestion to study feeding by an oribatid mite species in pine litter. He estimated both I and k simultaneously by fitting data on accumulation of radioactivity to equation (3). Crossley et al. (1969) analyzed fluctuations in ^{137}Cs content of arthropods in litter following inputs of radioactive tracer arising from autumnal leaf drop. Crossley (1969) utilized three radioisotopes for simultaneous independent estimates of feeding rate by arthropods in an herbaceous ecosystem.

Crossley et al. (1970) measured energy assimilation by a cricket (*Acheta domesticus* L.) with radioactive chromium. Since chromium is virtually unassimilated, a change in the ratio of calories to chromium in food and in feces was due to assimilation of energy by the insect.

Microcosm experiments

The use of small microecosystems (microcosms) in laboratory experiments allows for the systematic investigation of effects of environmental variables or interactions between ecosystem compartments. Studies of the dynamics of energy or radioactive tracers in microcosms provide a means for evaluating the influences of variables or compartments. Microcosms are analogs of natural systems, and permit experimental manipulations which would be difficult to do under field conditions. However, results may not be applicable to natural systems if the microcosms are not adequate representations of natural systems (Ragsdale, 1968).

Patten et al. (1967) measured ^{134}Cs transfers in microcosms of increasing complexity. Components were white oak (*Quercus alba* L.) leaves, microflora, millipedes (*Dixidesmus erasus* Loomis) and mineral soil. Analog computer simulation of the experimental results was the primary means of interpretation. Movement of ^{134}Cs in the microcosms was markedly influenced by the biota. Feeding performances of the millipedes was significantly better in microcosms containing mineral soil. Witkamp et al. (1969) continued these studies and increased their complexity by adding snails (*Paravitrea* sp.) and green plants (*Amorpha fructicosa* L.). Microcosms demonstrated such phenomena as microbial immobilization of the ^{134}Cs, and increased ^{134}Cs movement due to feeding by snails or millipedes and results of competition between them.

Kowal et al. (1970) used microcosms to estimate ingestion rates of microarthropod groups feeding in ^{45}Ca tagged pine (*Pinus echinata* Mill.) litter. Either the L, F_1, F_2 or H layer was tagged in microcosms containing complete litter-soil layers and entire microarthropod faunas. Replicate microcosms were sacrificed every 5 days during a 60-day period. Estimates of feeding by microarthropods, based on their accumulations of ^{45}Ca, revealed rates and locations of feeding activities. For "total saprovores," about 41 percent of ingestion was in the L layer, 39 percent in the F_1 layer, and only about 20 percent in the F_2 and H layers. Entomobryid collembolans, jumping surface dwellers, obtained 52 percent of their food from the L layer. Poduromorphs, nonjumping forms, were found to ingest more of the lower layers. About 39 percent of their food originated in F_2 and about 16 percent in H layers.

These examples illustrate the type of information which can be obtained with combined microcosm-radiotracer experiments. Hopefully, experiments and measurements on real, natural systems will confirm the detailed information so readily obtained in microcosms.

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